

Temperature and Trinexapac-Ethyl Effects on Bermudagrass Growth, Dormancy, and Freezing Tolerance

Matthew J. Fagerness,* Fred H. Yelverton, David P. Livingston, III, and Thomas W. Rufty, Jr.

ABSTRACT

Applications of the plant growth regulator (PGR) trinexapac-ethyl [4-(cyclopropyl- α -hydroxymethylene)-3,5-dioxocyclohexane carboxylic acid ethylester] (TE) can delay winter dormancy in 'Tifway' bermudagrass (*Cynodon dactylon* var. *dactylon*), which suggests a response to TE when temperatures are suboptimum for bermudagrass growth. The purpose of this study was to investigate the interactive role of temperature and TE in bermudagrass growth responses, dormancy, and freezing tolerance. Trinexapac-ethyl (0.11 kg a.i. ha⁻¹) was applied in two growth chamber experiments, and across a 2-yr period in the field. Results indicated that TE reduced vertical shoot growth and increased stolon production, turf density, and quality when applied at high temperatures (35–36°C). While TE effectively reduced vertical shoot growth at low (20–22°C) temperatures, little impact on stolon development was observed under these conditions. Autumn applications of TE when temperatures were cool (\approx 25°C) at the time of application led to decreased turfgrass density and quality. These responses may explain the effectiveness of using TE to aid in bermudagrass transition to overseeded cool-season grasses and were probably due to the limited ability of bermudagrass to recover from initial post-application growth reduction and observed leaf chlorosis. Observed delayed autumn dormancy due to summer applications of TE and accelerated dormancy due to late-season applications did not conclusively relate to the freezing tolerance of bermudagrass.

BERMUDAGRASS (*Cynodon* spp.) is the most commonly grown warm-season turfgrass species in the southeastern USA. Aggressiveness of bermudagrass is attributable to a C-4 carbon assimilation pathway and to rhizomatous and stoloniferous growth habits (Beard, 1973). The ability of bermudagrass to grow rapidly, both vertically and horizontally, has led to the extensive use of PGRs, which effectively control the growth of numerous turfgrass species (Johnson, 1990). Several PGRs are available for use on bermudagrass which inhibit the biosynthesis of gibberellic acid (Watschke, 1985; Kaufmann, 1986), and include flurprimidol [α -(1-methylethyl)- α -(4-(trifluoro-methoxy)phenyl)-5-pyrimidine-methanol], paclobutrazol [(+/-)-(R*,R*)- β -[(4-chloro-phenyl)methyl]- α -(1,1-dimethylethyl)-1H-1,2,4-triazole-1-ethanol], and TE. Multiple applications of PGRs often are required for effective long-term growth inhibition, as warm-season grasses have the potential for rapid growth over an extended period of time (Johnson, 1990, 1992a, 1994; Fagerness and Yelverton, 2000).

Although the main purpose for PGR applications to

bermudagrass is to slow growth during the high temperature periods of summer, there are some indications that additional types of effects can occur with their use. Recent research suggests that summer applications of TE may delay the onset of Tifway bermudagrass dormancy (Fagerness and Yelverton, 2000). Also, applications of TE near the end of the bermudagrass growing season can be used to aid overseeding by assisting transition to the cool-season species. Preliminary field observations, however, suggest that late season TE applications might lead to negative effects on bermudagrass freezing tolerance (Fagerness and Yelverton, 1999).

Because of the extended seasonal use of PGRs in the field, it is important to understand PGR interactions with temperature. Temperature effects on growth of bermudagrasses have been reported (Satorre et al., 1996; Unruh et al., 1996), but no studies have examined temperature and growth regulator interactions. The main objective of this study was to investigate growth of bermudagrass in response to TE under different temperature regimes and during the transition into winter dormancy. We also examined whether TE treatments altered the freezing tolerance of bermudagrass.

MATERIALS AND METHODS

Growth Chamber Experiments

Experiments were conducted at the North Carolina State University Southeast Plant Environmental Laboratory, Raleigh, NC, to examine TE and temperature effects on the growth of Tifway bermudagrass. Environmental growth chambers were programmed to establish high and low day/night growth temperatures. High temperatures were either 35/25°C or 36/31°C, and low temperatures were either 20/10°C or 22/17°C. Preliminary experiments indicated that similar treatment differences occurred in the aforementioned high and low temperature ranges. All growth chambers had a 14-h photoperiod, with a mean irradiance of 1200 μ mol photons m⁻² s⁻¹.

For experiments measuring clipping biomass, field samples were collected as 10-cm diameter sod cores, all from a uniform bermudagrass stand at the Sandhills Research Station, Jackson Springs, NC. Soil was a Wakulla sand (siliceous, thermic Psammentic Hapludults) with 94% sand, 4% silt, 2% clay, 24 mg g⁻¹ organic matter, and a pH of 6.1. Samples were placed in 15-cm diameter plastic pots, and the pots were backfilled with soil from the collection site. All samples received daily irrigation and monthly fertilizer applications at the equivalent of 50 kg N ha⁻¹. Plant cultures were acclimated to growth temperatures at least 2 wk before PGR treatments were applied and mowing height was maintained at \approx 1.9 cm.

Trinexapac-ethyl (120 g a.i. L⁻¹ emulsifiable concentrate) was applied to sod cores 3 wk after their introduction to growth chambers at a rate of 0.11 kg a.i. ha⁻¹ using a CO₂-pressurized

Matthew J. Fagerness, Dep. of Horticulture, Forestry, and Recreation Resources, Kansas State Univ., Manhattan, KS 66506-5507; Fred H. Yelverton and Thomas W. Rufty, Jr., Crop Science Dep., 100 Derieux St.; and David P. Livingston, III, USDA-ARS and Crop Science Dep., 840 Method Rd. Unit 3, North Carolina State Univ., Raleigh, NC 27695-7620. Received 5 July, 2001. *Corresponding author (mfagerne@oznet.ksu.edu).

(179 kPa) spray chamber with a water carrier volume of 304 L ha⁻¹. The bermudagrass was mowed to a height of 1.9 cm three times weekly for 7 wk. Clippings were oven-dried at 70°C for 72 h and then weighed.

Trinexapac-ethyl effects on lateral growth of bermudagrass stolons were examined using 10-cm sod cores taken from the North Carolina State University Turfgrass Field Laboratory, Raleigh, NC. Soil was a Cecil sandy loam (fine, kaolinitic, thermic Typic Kanhapludults) with 75% sand, 15% silt, 10% clay, 29 mg g⁻¹ organic matter, and a pH of 5.6. Samples were placed into 26-cm diam pots, backfilled with native soil, and placed into the growth chambers as before. Trinexapac-ethyl was applied 3 wk after introduction to growth chambers at a rate of 0.11 kg a.i. ha⁻¹, using the same application parameters as previously described. Beginning 1 wk after treatment (WAT) and continuing through 8 WAT, lateral growth was estimated by counting the number of stolons emerging from the central sod core.

Field Experiment

Experiments were conducted in 1997 and 1998 at the Sandhills Research Station in Jackson Springs, NC, on bermudagrass plots established in June 1995. Soil was a Wakulla sand. Turf was vertically mowed each spring, received urea at 50 kg N ha⁻¹ mo⁻¹ from May through September of each year, and was irrigated as needed. Turf was maintained to a height of 1.9 cm.

Treatments were intended to simulate recommended application practices for TE in North Carolina. Spray applications were made at four separate timings in each of two growing seasons. Initial applications were made 2 July 1997 or 25 June 1998 when the bermudagrass was actively growing. Sequential applications at 4-wk intervals were made on 1 Aug. 1997 or 23 July 1998 and again on 26 Aug. 1997 or 21 Aug. 1998. The late applications of TE were made to previously nontreated turf on 23 Sept. 1997 or 18 Sept. 1998 with the intent of simulating TE use as an overseeding aid. Spray pressure and water carrier volume were 179 kPa and 562 L ha⁻¹, respectively. Wind speed was negligible for all applications. Plots were 1.5 m by 6.0 m, and were arranged in a randomized complete block design with four replications.

Turfgrass quality was evaluated on five occasions between 25 Sept. and 25 Nov. (13, 14, 16, 18, and 20 WAT). Visual quality ratings were a function of turfgrass color, texture, and density and were based on a 1 to 9 scale (1 = dead or fully dormant turf, 9 = ideal turf, and 5 = minimally acceptable turf). Late-season growth parameters were assessed three times during the autumn at monthly intervals, beginning in late September when the 12 WAT application of TE was made. Shoot density and rooting were measured in two areas within each plot to reduce replicate variance. Shoot density was assessed using a 2-cm² counting frame and extrapolating for a 1-m² area. Root mass was assessed by collecting two 1600-cm³ cores plot⁻¹. Soil was separated from the shoots and thatch layer, and soil was removed from root tissue by sieve-washing. The root tissue was oven-dried for 72 h at 70°C, preweighed in a ceramic crucible, and placed in a muffle furnace, which incinerated all organic material across a 12-h period at 500°C. Root biomass was calculated from crucible weight before and after incineration.

Freezing tolerance was based on rhizome and stolon (i.e., sprigs) survival and subsequent regrowth. Samples were collected for each treatment in mid-October (16 WAT) and again in mid-November (20 WAT) of both years to determine survivability at two different degrees of autumn dormancy. Eight segments of rhizomes and stolons, each with at least one node,

were separately planted into potting soil in 1.9-cm diam. containers. Sprigs were chilled at 3°C for 21 d to allow sufficient development of cold hardiness (Beard, 1973). Selected sprigs were packed in crushed ice to prevent tissue super-cooling while being frozen to -5°C, with a temperature decrease of 1°C h⁻¹. Sprigs were maintained at the target freezing temperature for 3 h before being returned to 3°C, with a temperature increase of 2°C h⁻¹. Sprigs exposed to freezing temperatures, along with control samples that were chilled but not frozen, were then replanted in potting soil. Samples were maintained at 25°C and monitored for new growth one and three weeks after the freezing events. Growth and therefore survival were qualified as emergence of new leaf tissue from nodes.

Statistics

Each growth chamber experiment featured TE as the second factor, completely randomized and replicated within each growth temperature environment. Treatments were replicated four times in each growth chamber experiment. Stolon numbers in the lateral growth experiment also were analyzed relative to initial values. Growth chamber experiments were not replicated over time, due to the high level of available environmental control.

All data from the field experiments were initially tested for variable TE effects across years, and the presence of interactions prevented pooling of data from 1997 and 1998. Freezing tolerance data were analyzed as a function of TE treatment and two separate harvest dates, while field data were analyzed as a function of only TE treatments.

Statistical analyses for all experiments were based on Analysis of Variance, using the SAS General Linear Model procedure (SAS Institute, 2000). Standard *F*-tests in all analyses were used to determine significance of main effects and interactions. Means separation using Fishers Protected Least Significance Difference test was employed when *F*-tests indicated significance at *P* > 0.05.

RESULTS

Growth Chamber Experiments

The high and low temperature treatments resulted in distinctly different rates of bermudagrass shoot biomass production throughout the experiment for non-TE-treated controls (Fig. 1). Significantly faster growth occurred at the higher growth temperature, with biomass at least two times greater at 35/25°C than at 20/10°C at the end of 7 wk. Trinexapac-ethyl reduced bermudagrass growth at both temperatures 1 WAT (Fig. 2). The TE effects tended to be greater at the lower temperature for the first 2 wk. Growth in both treatments began to increase after 2 to 4 wk and approached that of non-TE-treated bermudagrass toward the end of the experiment.

Bermudagrass stolon growth was assessed under a broader range of growth temperatures than for the biomass production experiment to further test bermudagrass responses to high and low temperature extremes. The two temperature environments discussed from each experiment thus differed, but were chosen based on a similar response in preliminary studies at both the high and low temperature treatments. The number of stolons developing across time was affected by both growth temperature and TE (Fig. 3). In the non-TE-treated controls, the number of stolons was much higher at the

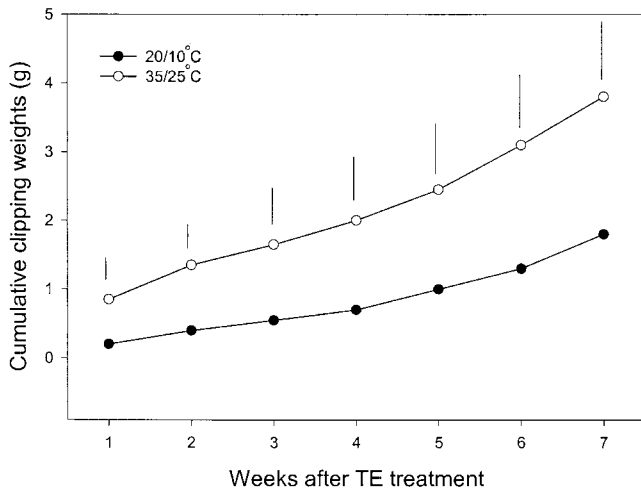


Fig. 1. Growth temperature effects on non-TE-treated 'Tifway' bermudagrass shoot biomass. First exposure to growth temperatures was 3 wk prior to initial application of trinexapac-ethyl (TE) at a rate of 0.11 kg a.i. ha⁻¹. Vertical lines above each time point represent calculated Fisher's Protected LSD values at $P = 0.05$.

higher growth temperature (36/31°C) and steadily increased with time. Four weeks after TE application, about twice as many stolons had emerged from sod cores treated with TE at 36/31°C, when compared with the non-TE-treated control. Conversely, stolon number was unaffected by TE at 22/17°C.

Field Experiment

Field experiments were used to evaluate TE effects on late-season turf quality and cold temperature sensitivity. Because of the impact of temperature on bermudagrass growth seen in the growth chamber experiments, field temperatures were of particular interest in interpreting results. Mean aerial temperatures from the Sandhills Research Station in 1997 and 1998 are shown in Fig. 4. As normally done with bermudagrass in this geographical region, there were 3 applications of TE during the

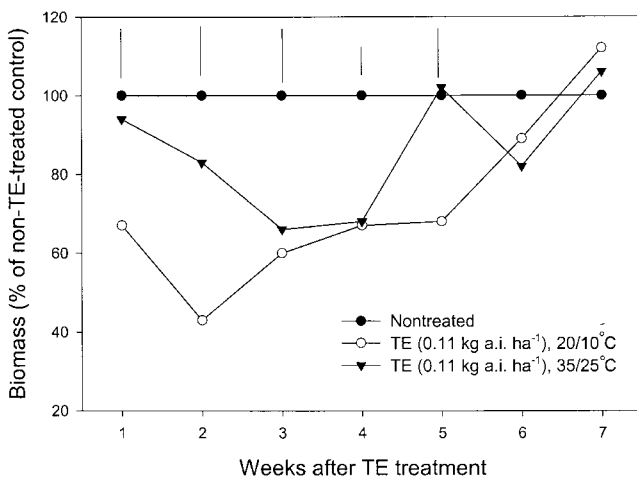


Fig. 2. Relative trinexapac-ethyl (TE) effects on shoot biomass at 20/10°C or 35/25°C. Trinexapac-ethyl was applied at a rate of 0.11 kg a.i. ha⁻¹ 1 wk prior to initial measurements. Vertical lines above significant time points represent calculated Fisher's Protected LSD values at $P = 0.05$.

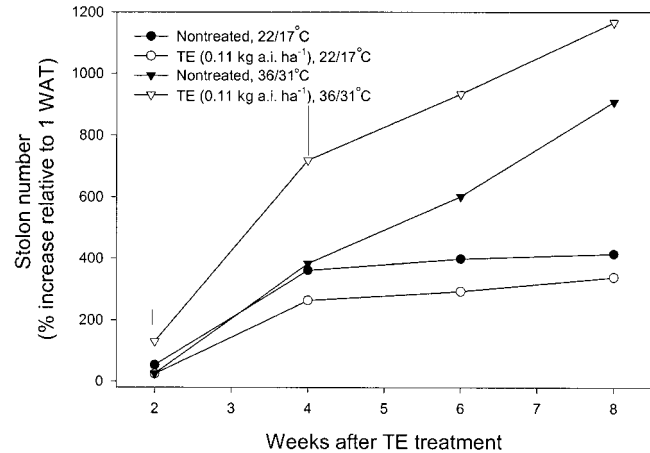


Fig. 3. Effects of growth temperature and trinexapac-ethyl (TE) on the number of stolons emerging from the central core of transplanted bermudagrass sod. Vertical lines above each time point represent calculated Fisher's Protected LSD values at $P = 0.05$.

warmest periods of summer. A late-season treatment was applied later to previously nontreated turf. Temperatures in 1997 were noticeably cooler than in 1998 over the entire growing season. The late-season treatment was applied when air temperatures were 8 to 10°C cooler than for the summer treatments.

Visual turf quality patterns in the autumn differed in the 2 yr of the experiment. Visual quality tended to decline in all treatments as the turf moved towards dormancy in 1997 (Fig. 5). Plots receiving the three seasonal applications of TE exhibited enhanced turfgrass quality throughout the experiment. In contrast, the single late-season application of TE resulted in reduced turfgrass quality, when compared with the non-TE-treated control. Reduced quality was a function of both suppressed growth and mild chlorosis observed in the leaves. The described response to the 1997 late-season TE application did not occur to the same extent in 1998. With a similar late-season treatment schedule, there was an initial reduction in turfgrass quality 13 WAT in 1998, but the effect dissipated and there were no further dis-

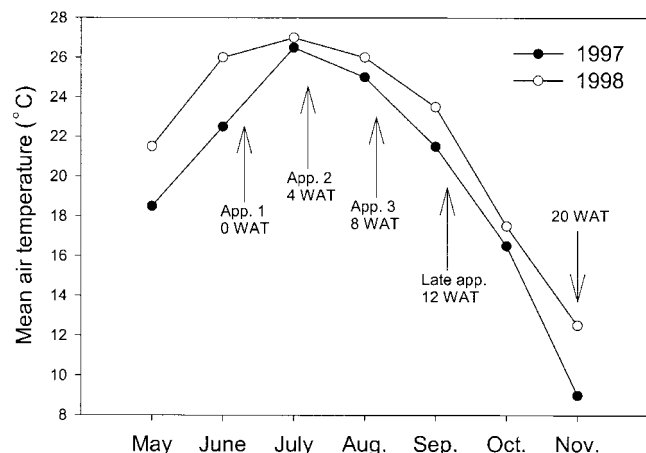


Fig. 4. Mean air temperatures from May to November 1997 and 1998 at the Sandhills Research Station. Vertical arrows indicate timings for trinexapac-ethyl applications at 0, 4, 8, and 12 wk after treatment (WAT).

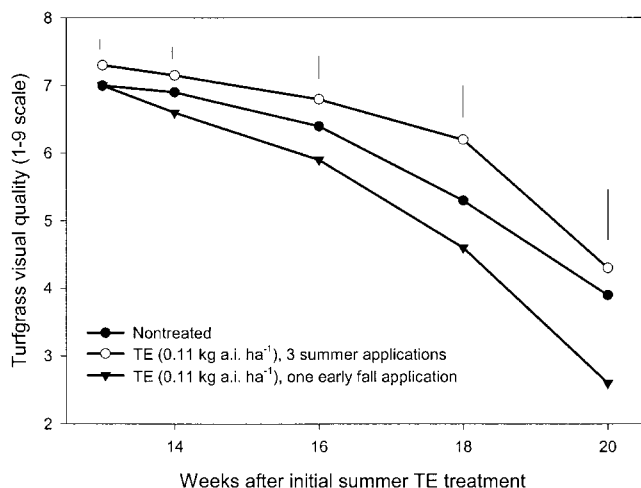


Fig. 5. Effects of trinexapac-ethyl (TE) on bermudagrass visual quality during the 1997 growing season. Quality was assessed using a 1 to 9 scale (1 = dead or fully dormant turf, 9 = ideal turf, and 5 = minimally acceptable turf). Vertical lines above each time point represent calculated Fisher's Protected LSD values at $P = 0.05$.

cernible quality differences after that time (data not shown).

Shoot density in 1997 was not affected greatly by TE. With three seasonal applications of TE, there was a small reduction in shoot density at 12 WAT (late September), but a small increase by 16 WAT (Table 1). The late-season TE application resulted in a decrease in shoot density at 16 and 20 WAT, when compared with the control. Shoot density was not affected by TE in 1998 (data not shown). Three seasonal applications of TE resulted in increased root biomass at 12 WAT, when compared with samples collected from non-TE-treated control plots (Table 1). However, no significant effects were detectable beyond 12 WAT. The late-season treatment with TE had little impact on root biomass.

Sprigs harvested from plots in the autumn of 1997 and 1998 were subsequently used for freezing tolerance studies. Results from these studies showed that, regardless of TE treatment, whether or not sprigs were exposed to the -5°C temperature had the most consistent main effect on sprig freezing survival (Table 2). Interactions between harvest date and temperature for both rhizomes and stolons in 1998 showed increased sprig tolerance to the -5°C temperature after the November harvest (Table 3). Results therefore supported patterns of natural bermudagrass progression into winter dor-

Table 1. Bermudagrass shoot density and root biomass as influenced by summer and late-season applications of trinexapac-ethyl (TE) in 1997.

Treatment	Weeks after treatment		
	12	16	20
	Shoot density		
	shoots $\text{m}^{-2}\dagger$		
Nontreated	118 000	110 000	111 250
TE (3 applications) \ddagger	98 750	137 500	125 000
TE (late) \ddagger	117 750	97 500	87 500
LSD $_{0.05}\S$	14 021	14 204	29 206
	Root biomass		
	g $1600\text{ cm}^{-3}\P$		
Nontreated	1.98	2.76	1.78
TE (3 applications)	3.71	2.78	2.78
TE (late)	3.71	2.79	2.19
LSD $_{0.05}\S$	0.98	ns	ns

\dagger Means for shoot density were based on two samples per plot, measured with a 2-cm² counting frame. Means for Tifway root biomass were pooled across both years of the experiment and were derived from measurements of two samples per plot.

\ddagger Initial application in early summer followed by two sequential applications at 4-wk intervals. The late TE treatment was applied in early autumn during each year of the experiment.

\S LSD $_{0.05}$ values indicate significant means separation, based on standard F tests at $\alpha = 0.05$.

\P Rooting data were pooled across 1997 and 1998.

mancy, with expected increases in freezing tolerance as autumn progressed.

Although TE did not affect freezing tolerance, a harvest date \times TE treatment interaction was observed in the autumn of 1998 for stolon freezing tolerance (Table 2). With three summer applications of TE or a single late-season application, an increase in stolon freezing tolerance was evident after the October harvest (Table 3). Neither of these two TE applications affected stolon freezing tolerance by November.

DISCUSSION

The primary objective of this study was to determine if the impact of TE was altered when applied at different air temperatures. This research indicated that temperature and TE interactions existed. Before initiating the experiments, it seemed reasonable to believe that TE effects would be more pronounced at higher temperatures because of the greater potential for growth reduction when growth is more rapid. In the growth chamber experiments, however, temperature data revealed that TE suppressed growth at both high and low tempera-

Table 2. Probability values for trinexapac-ethyl (TE) treatment, harvest date, and chilling temperature effects on bermudagrass stolon and rhizome freezing tolerance.

Experimental factor \dagger	1997		1998	
	Rhizomes	Stolons	Rhizomes	Stolons
	Probability $> F$			
Hardening temperature \ddagger	0.0021	0.0002	ns \S	0.0001
Harvest date	ns	ns	ns	0.0001
TE treatment	ns	ns	ns	ns
Harvest date by temperature	ns	ns	0.0316	0.0001
Harvest date by TE-treatment	ns	ns	ns	0.005

\dagger Probability values are from an Analysis of Variance performed on treatments arranged as a 3-factor factorial.

\ddagger The hardening temperature to which sprigs were exposed was either 3 or -5°C .

\S ns = not significant.

Table 3. Bermudagrass stolon freezing tolerance as influenced by harvest data and trinexapacethyl (TE) in 1998.

Treatment	Harvest	Stolon survival
		%
Nontreated	October	22
TE (3 applications)†	October	41
TE (late)‡	October	56
Nontreated	November	81
TE (3 applications)	November	81
TE (late)	November	69
LSD _{0.05} §		16

† Means were calculated from eight samples within each temperature and treatment.

‡ Initial application in early summer followed by two sequential applications at 4-wk intervals. The late TE treatment was applied in early fall during each year of the experiment.

§ Fisher's Protected LSD Test was conducted based upon a *P*-value > *F* of 0.005 for the harvest × treatment interaction means shown.

tures and growth suppression was greater at the lower temperature (Fig. 2).

The mode of action for gibberellic acid inhibitors like TE involves accumulation of active ingredient molecules at the intercalary meristem region, subsequent inhibition of gibberellin biosynthesis, and slowing of cell expansion in sheaths and basal regions of leaves (Kaufmann, 1986). Greater TE growth suppression at lower temperatures would suggest that TE catabolism was reduced or that the TE biochemical effects were simply more effective with slower rates of cell division and expansion associated with slower growth. It should be emphasized that biomass production was estimated from clippings and thus only reflected TE suppression of vertical leaf and shoot growth.

The growth chamber experiments showed that TE effects on lateral growth also were temperature dependent, but different from those on vertical growth. Bermudagrass produced higher stolon numbers at higher temperatures regardless of TE treatment, as shown by the comparison to non-TE-treated controls on the last two sampling dates (Fig. 3). This relationship was not unexpected, as a positive correlation between increasing temperature and development of stolons and rhizomes was reported previously for bermudagrass (Satorre et al., 1996). The TE treatment increased stolon numbers, but only when plants were growing at higher temperatures. The TE effect on stolon growth was noticeable within 2 WAT and quite pronounced at 4 WAT. The observed increases in autumn shoot density in the field following multiple TE applications during the warm summer months also reflected increases in lateral shoot development.

It is not clear why TE increased stolon growth only at higher temperature. However, physiological relationships can be considered that might explain the response. Temperature establishes the potential for stolon development (Satorre et al., 1996). Another factor known to influence lateral development in grass species is N nutrition. Higher rates of N uptake and assimilation have been shown to stimulate tiller development (Auda et al., 1966; Simon and Lemaire, 1987; Thompson and Clark, 1993; Belanger, 1998). It is likely that higher bermudagrass growth rates at higher temperatures are associated with greater rates of N uptake and delivery

to shoots. Thus, higher temperatures and more rapid N uptake likely stimulated lateral meristems and increased growth of the stolons. Following treatment with TE, vertical shoot growth suppression would lead to increased allocation of resources (e.g., more N and carbohydrates to lateral meristems), further enhancing the process.

Our experiments indicate that temperature also may play a role in TE effects on dormancy. The process of dormancy, and the physiological basis for it, is still largely undefined (van der Schoot, 1996). It was observed previously that three summer applications of TE could delay the onset of bermudagrass dormancy (Fagerness and Yelverton, 2000). The pattern also was observed in the first year of this study (Fig. 4 and Table 1), when turf treated with three TE applications consistently had higher quality and shoot density, while dormancy in non-TE-treated control turf progressed. In contrast, the 1997 single late-season TE application led to decreases in shoot density (Table 1) and visual quality (Fig. 4), indicating a more rapid progression into dormancy.

Field studies have indicated that TE can discolor bermudagrass when applied in the summer months (Johnson, 1992b; Wiecko, 1997; Fagerness and Yelverton, 2000). Bermudagrass recovers quickly, however, under favorable temperature and growth conditions. One explanation for the negative effects resulting from the autumn TE application in 1997 (Fig. 5) is that the turfgrass was more sensitive to TE. The late-season application occurred when mean daily temperatures were ≈8°C cooler than those in the July to August period. Bermudagrass was growing relatively slowly and beginning the transition into dormancy, which may have amplified the initial effects of TE applied that late in the growing season.

Temperature and TE interactive effects on root growth were largely inconclusive. Multiple TE and late TE treatments resulted in greater root mass at 12 WAT (end of September), but the growth stimulation was not obvious later on. The root growth response appeared to depend on active bermudagrass growth, as the lack of an effect at later dates coincided with the progression into dormancy (Fig. 5). It should be emphasized that the method of root recovery is relatively imprecise. The procedure does not distinguish inactive from active roots; therefore it cannot define the actual root growth status at a particular time.

The absence of TE effects on autumn visual quality and density in the second year (1998) was unexpected. It is conceivable that this response was due, in part, to higher growth temperatures. Air temperature monitoring showed that seasonal temperatures were higher throughout 1998 (Fig. 5). Since air temperatures were higher at the time of the late-season application in 1998, growth regulating effects of TE may have been offset by more rapid bermudagrass growth.

Variable growth temperatures between 1997 and 1998 corresponded with changes in sprig freezing tolerance between the two seasons. Cooler autumn temperatures in 1997 stimulated the natural development of cold har-

diness (Beard, 1973), which may have accounted for the absence of any TE effects on autumn freezing tolerance. Conversely, warmer autumn temperatures in 1998 would more likely have delayed the development of cold hardiness and thus predisposed stolons and rhizomes to freezing injury. Increased stolon freezing tolerance 4 wk following a 1998 late-season application of TE may therefore have been facilitated by the growth inhibiting effects of TE. The continuance of warmer autumn temperatures through November 1998 also may have accounted for the same tissues being more susceptible to freezing injury, at a time when the effects of TE would have dissipated.

In summary, field TE treatments at different times during the year can lead to different types of vegetative growth responses that can be attributed, at least in part, to interactions with temperature. From a turfgrass management perspective, TE effects tended to be positive at higher temperature, with slower growth accompanied by increased density and quality. At lower temperatures, TE still had strong effects on growth, but bermudagrass may have difficulties recovering from the initial suppressive effects of TE. Applications of TE in the autumn can result in decreased competitiveness because of slower growth and decreased density. Slower growth and decreased density apparently are the mechanistic basis for enhanced transition to an overseeded cool-season species.

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